The influence of historical climate changes on Southern Ocean marine predator populations: a comparative analysis

Running head: Southern Ocean predator palaeoecology

Authors: J. L. Younger[1], L. M. Emmerson[2] & K. J. Miller[3,4]

Author affiliations:

1. Institute for Marine and Antarctic Studies, University of Tasmania, Private Bag 129, Hobart 7001, Tasmania, Australia.
2. Australian Antarctic Division, 203 Channel Highway, Kingston 7050, Tasmania, Australia.
3. Australian Institute of Marine Science, The UWA Oceans Institute, 35 Stirling Highway, Crawley, WA 6009, Australia.
4. School of Biological Sciences, Private Bag 5, University of Tasmania, Hobart 7001, Tasmania, Australia.

Corresponding author contact information:

Jane Younger

Jane.Younger@utas.edu.au

Institute for Marine and Antarctic Studies, University of Tasmania, Private Bag 129, Hobart 7001, Tasmania, Australia. Phone: +61 439 869 364

Keywords: climate change ecology; palaeoecology; Antarctic; sub-Antarctic; polynya; penguin; pinniped; Holocene; palaeoclimate

Paper type: Research Review

Abstract

The Southern Ocean ecosystem is undergoing rapid physical and biological changes that are likely to have profound implications for higher-order predators. Here we compare the long-term, historical responses of Southern Ocean predators to climate change. We examine palaeoecological evidence for changes in the abundance and distribution of seabirds and marine mammals, and place these into context with palaeoclimate records in order to identify key environmental drivers associated with population changes. Our synthesis revealed two key factors underlying Southern Ocean predator population changes; 1) the availability of ice-free ground for breeding, and 2) access to productive foraging grounds. The processes of glaciation and sea ice fluctuation were key; the distributions and abundances of elephant seals, snow petrels, gentoo, chinstrap and Adélie penguins all responded strongly to the emergence of new breeding habitat coincident with deglaciation and reductions in sea ice. Access to productive foraging grounds was another limiting factor, with snow petrels, king and emperor penguins all affected by reduced prey availability in the past. Several species were isolated in glacial refugia and there is evidence that refuge populations were supported by polynyas. While the underlying drivers of population change were similar across most Southern Ocean predators, the individual responses of species to environmental change varied because of species specific factors such as dispersal ability and environmental sensitivity. Such interspecific differences are likely to affect the future climate change responses of Southern Ocean marine predators and should be considered in conservation plans. Comparative palaeoecological studies are a valuable source of long-term data on species' responses to environmental change that can provide important insights into future climate change responses. This synthesis highlights the importance of protecting productive foraging grounds proximate to breeding locations, as well as the potential role of polynyas as future Southern Ocean refugia.

55 # Introduction

56 Southern Ocean marine ecosystems have undergone rapid physical changes in recent decades,
57 including increases in air and ocean temperatures, changes in the extent and seasonality of
58 sea ice, decreasing salinity, and poleward shifts of oceanographic fronts (Böning *et al.*, 2008,
59 Bracegirdle *et al.*, 2008, Sokolov & Rintoul, 2009, Stammerjohn *et al.*, 2012, Turner *et al.*,
60 2009, 2014). In turn, the changes in the physical environment are driving change in marine
61 biota at all trophic levels, including fish, cephalopods and zooplankton such as Antarctic krill
62 (*Euphausia superba*), all of which are important prey species for higher-order predators such
63 as seabirds and marine mammals (Atkinson *et al.*, 2005, Constable *et al.*, 2014). Further
64 physical changes are projected by climate models into the future (Collins *et al.*, 2013a).
65 Collectively, these changes are likely to have profound implications for Southern Ocean
66 marine predators, with effects varying by both species and location, and expected to impact
67 both breeding habitat and marine foraging grounds (Constable *et al.*, 2014, Smetacek &
68 Nicol, 2005).

69 The ongoing physical and biological changes in the Southern Ocean are the result of a
70 marked shift in the Earth's environmental state (Lewis & Maslin, 2015). This shift is being
71 considered as the dawn of a new epoch, termed the Anthropocene, that is characterised by
72 changes to land, oceans, the atmosphere and evolutionary pressures (Lewis & Maslin, 2015).
73 The extinction rate during this new era is estimated at 100 to 1,000 times greater than in
74 previous epochs and is likely to result in a sixth mass extinction (Barnosky *et al.*, 2011). In
75 order to understand how species might respond to the unprecedented environmental change
76 predicted for the Anthropocene, we must consider not only their recent population trends over
77 decadal timescales, but also how they responded to similar long-term environmental regime
78 shifts in past epochs.

79 Evidence of species' histories can be found in various forms such as fossil remains and
80 genetic data. With the right tools this evidence can be used to build a picture of a species'
81 past ecology, known as palaeoecology, over periods of hundreds to millions of years (Seddon
82 *et al.*, 2014). Such palaeoecological evidence provides long-term insight into how species
83 have coped with environmental change in the past. Reconstructing historical trends in
84 abundance and distribution can provide clues about how specific environmental changes
85 affected populations, thereby increasing our understanding of species' environmental niches.
86 If a species was robust to past climate perturbations we might expect them to have good
87 resilience to future change, depending on the direction and pace of the environmental shift.
88 When combined with information on extant population structure and abundance, information
89 on the past processes that shaped population characteristics may enable predictions of how
90 species will respond as habitat availability and quality changes, and help us to assess the risk
91 of local or widespread extinction (Hoelzel, 2010, Seddon *et al.*, 2014). By comparing trends
92 for different species we can begin to understand which are the most important of these
93 environmental factors.

94 Predators have an integral role in regulating ecosystems via top-down processes (Baum &
95 Worm, 2009, Heithaus *et al.*, 2008); hence how they might respond to environmental change
96 is particularly important. For predators to prosper, productive foraging grounds must exist
97 within reach of suitable breeding habitat. However, what constitutes suitable marine foraging
98 grounds or terrestrial breeding sites varies by species due to differences in their foraging
99 modes and abilities, as well as the required physical characteristics of their breeding sites.
100 Both marine and terrestrial conditions are projected to change across the Southern Ocean, and
101 predator populations in both the sub-Antarctic and Antarctic are likely to be affected.
102 Potential mechanisms for these impacts include, but are not limited to: the loss of breeding
103 habitat in cases where predators use sea ice as a breeding platform; the influence of changing

104 sea ice seasonality on the timing of breeding; the effects of increasing temperatures for
105 species that are highly cold adapted; and changes in prey abundance, distribution and
106 accessibility. Different populations of the same species are likely to experience different
107 impact mechanisms due to regional variation in environmental trends.

108 Here, historical changes in populations of Antarctic and sub-Antarctic marine predators,
109 specifically seabirds and mammals, are reviewed, compared and placed into context with past
110 environmental changes. We focus on predators with breeding sites that are distributed in and
111 around mainland Antarctica, its offshore islands and the sub-Antarctic islands, because these
112 species utilise the Southern Ocean for both breeding and foraging. Migratory species that
113 periodically reside in the Southern Ocean, including cetaceans, are excluded. In order to
114 restrict our study to purely environmental driven responses, only changes in predator
115 populations that occurred prior to anthropogenic impacts, defined here as 1610 to coincide
116 with the proposed inception of the Anthropocene (Lewis & Maslin, 2015), are considered.

117 ## An overview of Southern Ocean palaeoclimate

118 The Pleistocene geologic period (2.588 mya to 11.7 kya) (Cohen *et al.*, 2013) was
119 characterized by large-scale global climate oscillations, varying from cold periods of
120 glaciation to warmer interglacial periods (Figure 1) (Jouzel *et al.*, 2007). Changes in the
121 Southern Ocean environment throughout the Pleistocene have been reconstructed using a
122 variety of methods, including ice cores, marine and lake sediment cores, and lithology. The
123 last glacial maximum (LGM, 26 – 19.5 kya) marks the most recent time of maximum ice
124 sheet extent in Antarctica (Clark *et al.*, 2009). During the LGM, air temperatures were *ca.*
125 13°C colder than the present day (Jouzel *et al.*, 2007) and glaciation was extensive, with most
126 of the continental shelf covered by either marine-based ice sheets or thick, perennial sea ice

(Figure 2) (Anderson *et al.*, 2002, Bentley *et al.*, 2014, Gersonde *et al.*, 2005). Many sub-Antarctic islands were glaciated (Hodgson *et al.*, 2014) and surrounded by sea ice in the winter (Gersonde *et al.*, 2005). Oceanographic fronts, which are the boundaries between two water masses that tend to be associated with high prey abundance due to both enhanced local primary production and transport of prey to the front by currents (Bost *et al.*, 2009), were displaced northwards by around five degrees of latitude (Figure 2) (Gersonde *et al.*, 2005).

The dynamics of Antarctic sea ice are highly complex and can be described in terms of areal extent, concentration, thickness, formation rate and seasonality. Many of these variables are difficult to measure for contemporary sea ice, and reconstructing historical sea ice conditions is an ongoing challenge (Collins *et al.*, 2013b, de Vernal *et al.*, 2013). Fossils of diatom taxa that live in association with sea ice, and have particularly intense blooms at the ice edge, are preserved in marine sediments and can provide an excellent proxy for historical sea ice limits (Allen *et al.*, 2011, Gersonde & Zielinski, 2000). Diatom records are commonly used in Antarctic sea ice reconstructions, often coupled with other evidence such as lithology (Allen *et al.*, 2011), radiolarians (Gersonde *et al.*, 2005), or, more recently, highly branched isoprenoid biomarkers (Collins *et al.*, 2013b). Diatom records indicate that at its maximum extent during the last glacial period the circum-Antarctic winter sea ice field was approximately double its present area, extending to about 50°S (Figure 2) (Allen *et al.*, 2011, Collins *et al.*, 2012, Gersonde *et al.*, 2005). The extent of summer sea ice during the last glacial period is poorly constrained and an area of ongoing study (Collins *et al.*, 2013b), however, the data that are available suggest a northerly expansion to 55°S in some locations (Figure 2) (Allen *et al.*, 2011, Collins *et al.*, 2012, Gersonde *et al.*, 2005). Interestingly, the timing of the maximum extent of sea ice pre-dates the LGM (Allen *et al.*, 2011), with maximum winter and summer extents occuring at 25−23.5 kya and 31−23.5 kya, respectively (Collins *et al.*, 2012).

During the LGM, biological productivity south of the Polar Front was greatly reduced (Hillenbrand & Cortese, 2006), with estimates placing primary production at between two and five times less than current values (Kohfeld *et al.*, 2005). This estimate is inferred from export production records in sediment cores, where export production is the portion of primary production that accumulates in sediments (Kohfeld *et al.*, 2005). The low primary productivity during the LGM is likely to have had a regulatory effect on all trophic levels in the Southern Ocean food web by severely limiting the food resources that were available (Thatje *et al.*, 2008).

While overall biological productivity of the Southern Ocean was much reduced during the LGM, polynyas may have provided oases of productivity (Thatje *et al.*, 2008) and access points for predators amidst the extensive sea ice field. Polynyas are areas of open water within the sea ice field that are associated with enhanced primary production, due to an earlier spring melting of sea ice and a resultant earlier start in photosynthetic primary production (Martin, 2001). Coastal polynyas are formed by the outflow of katabatic winds that push sea ice away from the coastline, whereas open-ocean polynyas are generally formed by upwelling of warm, deep water associated with submarine geological formations such as seamounts (Comiso & Gordon, 1987, Holland, 2001, Martin, 2001, Thatje *et al.*, 2008). Sediment cores suggest the existence of LGM polynyas in several locations in the northern Weddell and Ross Seas (Figure 2) (Brambati *et al.*, 2002, Mackensen *et al.*, 1994, Smith *et al.*, 2010, Sprenk *et al.*, 2014, Thatje *et al.*, 2008). Polynyas could only have existed in the northern sections of the Weddell and Ross Seas because ice sheets covered large portions of these embayments during the LGM (Figure 2) (Anderson *et al.*, 2014, Hillenbrand *et al.*, 2014). Polynyas are thought to have been more widespread during the LGM due to a heightened intensity of katabatic winds (Smith *et al.*, 2010, Sprenk *et al.*, 2014), however the

sediment core record around Antarctica is sparse, so the locations of other LGM polynyas are currently unknown.

Following the LGM, warming temperatures saw the Southern Ocean shift away from glacial conditions and into the warm Holocene (11.7 kya to present, Cohen *et al.*, 2013) (Figure 1). The transition to the Holocene was characterised by retreating ice sheets, rising sea levels, increased seasonality of a decreasing sea ice cover, and increasing primary productivity (Allen *et al*., 2011, Anderson *et al.*, 2009, Barbara *et al.*, 2010, Bentley *et al.*, 2014, Collins *et al*., 2012, Crosta *et al.*, 2004, 2008, Denis *et al.*, 2009b, Gersonde *et al.*, 2005, Kohfeld *et al.*, 2005). These environmental responses to climatic changes happened asynchronously across the Southern Ocean. Throughout the Holocene there have been less dramatic fluctuations in local climate, including shifts in sea level, sea ice cover and some minor readvancement of glaciers.

Palaeoecology of the Southern Ocean

Evidence of palaeoecological processes can be found in a species' physical remains, including bone, tissue, eggshell or guano. Such evidence can be analysed using a combination of genetic, radioisotopic and geochemical methods, in order to study changes in distribution and abundance over thousands of years, identify locations of refugia and assess dietary changes. When combined with palaeoclimatic evidence, such as ice core and sediment records, it is possible to identify potential environmental drivers of population changes. In combination, these varied approaches can build a compelling picture of the past responses of Southern Ocean predators to environmental change.

Genetic studies using coalescent modelling allow for the estimation of changes in population size through time. In coalescent Bayesian skyline analysis, sequence data from multiple

individuals in a population are used to co-estimate genealogies and the effective population size at different points in time (Drummond *et al.*, 2005, Pybus *et al.*, 2000). If calibrating information such as ancient DNA, (see de Bruyn *et al.* (2011) for a comprehensive review), fossils or a known genetic mutation rate is available, the timings of these changes in abundance can be estimated and correlated with palaeoclimate records. A related method is the pairwise sequentially Markovian coalescent, which is used to estimate past population sizes using whole genome data from a single individual (Li & Durbin, 2011). This method is effective for estimating population sizes over long time scales (i.e. 100 kya to 10 mya), but is less accurate over shorter time scales compared to Bayesian coalescent methods, making these approaches complementary (Sheehan *et al.*, 2013).

Genetic data may also identify past refugia (Hewitt, 1996, 2000). Phylogenetic analyses can reveal genetically distinct lineages that may have arisen as a result of past isolation in refugia (Hewitt, 1996, 2000). Again, if the analyses can be calibrated, the timings of these events can be determined and the environmental drivers of isolation in refugia may be thus identified. Telltale patterns of genetic diversity may also be used to pinpoint the locations of past refugia; refugia are typically characterised by a pattern of clinal variation, decreasing with distance from the refuge, arising from founder effects as new areas are colonized following the expansion from the refuge (Hewitt, 1996, 2000).

Radiocarbon dating of organic remains, which can survive for thousands of years in the cold, dry Antarctic environment where microbial degradation is inhibited, can provide valuable palaeoecological data. The occupation history of the snow petrel (*Pagodroma nivea*) has been investigated by radiocarbon dating of solidified stomach oil, called mumiyo, which accumulates among rocks in breeding colonies (Hiller *et al.*, 1988). Dating of these deposits can provide a record of occupation at a given site. Radiocarbon dating of excavated penguin

guano sediments, called ornithogenic soils, that contain guano, eggshell fragments and bones can likewise be used to investigate occupation history (see Emslie *et al*., 2014 for a comprehensive review). Such studies may be supplemented with geochemical analyses of typical bio-elements found in penguin guano, which provide a proxy for the abundance of penguins (Sun *et al.*, 2000), and stable isotopic analyses of eggshells and guano can provide an understanding of diet through time (Emslie & Patterson, 2007, Emslie *et al.*, 2013). Finally, radiocarbon dated remains found outside a species' current range can provide clues to their distributions under different climatic regimes (Hall *et al.*, 2006).

Ice-free breeding species – the sub-Antarctic

The sub-Antarctic islands are populated by breeding colonies of many predators, including pinnipeds, penguins, petrels and albatrosses. Of these species, palaeoecological data are currently available for king penguins (*Aptenodytes patagonicus*) and Southern elephant seals (*Mirounga leonina*). Both species congregate in breeding colonies established on coastal ice-free ground; the king penguin breeds exclusively on sub-Antarctic islands between 45° and 55° south (Figure 3a) (Bost *et al.*, 2013), while the Southern elephant seal breeds mostly in the sub-Antarctic, with colonies also located in South America, the Antarctic Peninsula and maritime Antarctic islands, and in the Windmill Islands in East Antarctica (Figure 3b) (Heimark & Heimark, 1986, Lewis *et al.*, 2006, Murray, 1981). Both species are meso-predators with wide foraging ranges, extending to the edge of the pack ice in the case of the king penguin (Bost *et al.*, 2004, Moore *et al.*, 1999) and well into the sea ice zone in the case of the elephant seal (Charrassin *et al.*, 2008). Oceanographic fronts are important foraging grounds for both species (Bost *et al.*, 2009, Charrassin *et al.*, 2008). Elephant seals, king penguins and many other sub-Antarctic predators direct their foraging trips toward the Polar

246 Front, the sub-Antarctic Front or the Subtropical Front (Figure 2), as these areas provide a
247 predictable source of prey and good conditions for diving predators (Bost *et al.*, 2009).

248 **King penguins**

249 A genetic coalescent study of king penguins from the Crozet Archipelago revealed a rapid
250 population expansion closely following the end of the LGM (Trucchi *et al.*, 2014). The
251 Crozet king penguin effective population size increased from *ca.* 2,000 during the LGM to
252 *ca.* 170,000 today (Trucchi *et al.*, 2014). While many factors may have contributed to this
253 increase in abundance, the key ecological requirements for king penguins are year-round ice-
254 free breeding habitat and access to productive foraging grounds (Hunt, 1991). There is no
255 definitive evidence that Crozet was glaciated during the LGM, and estimates from sediment
256 core microfossil assemblages place the LGM sea ice field south of Crozet (Figure 3a),
257 although it should be noted that both the glacial history and the microfossil record in this
258 region are poorly resolved (Gersonde *et al.*, 2005, Hall, 2009, Hodgson *et al.*, 2014). Hence,
259 the overall indication is that ice-free breeding habitat was available on Crozet during the
260 LGM. It may therefore have been a lack of productive foraging that limited the size of the
261 king penguin population. As previously mentioned, biological productivity was likely much
262 reduced during the LGM (Hillenbrand & Cortese, 2006, Kohfeld *et al.*, 2005), furthermore,
263 the location of king penguin foraging grounds may have shifted during this time. King
264 penguins currently forage almost exclusively near frontal zones (Bost *et al.*, 2009). Crozet is
265 situated in the Polar Frontal Zone, equidistant (~400 km) from the Polar Front and the sub-
266 Antarctic Front, making it ideally positioned for king penguin foraging (Figure 3a) (Bost *et*
267 *al.*, 2009). However, it is likely that both of these fronts were displaced *ca*. 5-10° northwards
268 during the LGM (Figure 3a) (Gersonde *et al.*, 2005), possibly increasing the travel distance
269 from Crozet. The combination of shifted feeding grounds with lower overall biological

productivity may have reduced prey density to a level that was insufficient to support a large population of king penguins. Indeed, given the inherent variability in past population estimates, it is possible that no king penguins were present in the Crozet Archipelago during the LGM, and this colony was subsequently founded during the Holocene once conditions became more favourable. At present, palaeoecological studies of king penguins are limited to genetic coalescent data from a single colony (Table 1). The recovery of sub-fossil remains dating to the LGM would clarify the locations of king penguin colonies during the glacial period, and further genetic studies of other contemporary breeding colonies could indicate whether the Holocene population expansion on Crozet was an isolated trend, or occurred across the species' range.

Southern elephant seals

Southern elephant seals may have undergone a large latitudinal range expansion during the Holocene, taking advantage of emerging ice-free terrestrial habitat on the Victoria Land Coast in the Ross Sea *ca*. 7,000 years ago (de Bruyn *et al.*, 2009, 2014, Hall *et al.*, 2006). There is evidence for a mid-Holocene breeding colony and/or moulting site in the region, based on radiocarbon dated remains and genetic analysis (de Bruyn *et al.*, 2009, 2014, Hall *et al.*, 2006). Genetic evidence suggests the remains were most likely the remnants of a breeding colony, founded by individuals originating from Macquarie Island 2,500 km to the north, signifying a long distance colonisation event by a highly mobile species *ca*. 7,000 years ago (Figure 3b) (de Bruyn *et al.*, 2009, 2014). Elephant seal numbers then fluctuated in the Ross Sea region, until they eventually abandoned the area completely *ca*. 1,000 years ago, retreating to Macquarie Island (de Bruyn *et al.*, 2009, Hall *et al.*, 2006). However, while the genetic evidence suggests that the Ross Sea elephant seals were the constituents of a breeding population, the recovered remains were predominantly skin and hair, with only two pup

294 carcasses discovered (Hall *et al.*, 2006). Therefore, the possibility that this was a moulting
295 site rather than a breeding colony cannot be discounted, since elephant seal breeding sites
296 tend to contain large numbers of deceased pups, which have not been discovered so far at the
297 Ross Sea.

298 It has been postulated that the availability of ice-free breeding habitat, as determined by
299 glaciation, sea ice extent and seasonality, was the major limiting factor of elephant seal
300 distribution during the Holocene (de Bruyn *et al.*, 2009, Hall *et al.*, 2006). Elephant seals
301 currently maintain several small colonies on ice-free areas of the Antarctic Peninsula and
302 continent; however, no breeding or moulting sites exist within the Ross Sea region today,
303 with the Victoria Land Coast presently bounded by fast ice for the majority of the year,
304 thereby precluding the establishment of breeding colonies (Hall *et al.*, 2006). Beaches free of
305 glacial ice were probably released on the Victoria Land Coast between 8,000 and 7,500 years
306 ago, based on the grounding-line retreat of the Ross Sea ice sheet (Conway *et al.*, 1999).
307 Taylor Dome ice core records also indicate warmer conditions coincident with elephant seal
308 occupation of the Ross Sea (Monnin *et al.*, 2004), with these conditions possibly resulting in
309 reduced sea ice concentration in the area and therefore open water adjacent to the shore (Hall
310 *et al.*, 2006). Around 1,000 years ago, coeval with the final abandonment of the region by
311 elephant seals, glacial advance began to overrun the Holocene beaches (Baroni & Hall, 2004,
312 Baroni & Orombelli, 1991, 1994b) and methanesulfonic acid records from nearby Newall
313 Glacier indicate an increase in sea ice extent (Mayewski *et al.*, 1995). A contemporary study
314 of elephant seals from Macquarie Island indicated that increases in sea ice duration within the
315 seals' foraging range can have a negative influence on their abundance (van den Hoff *et al.*,
316 2014), therefore, the late Holocene increases in sea ice (Mayewski *et al.*, 1995) may have
317 directly contributed to elephant seals abandoning the Ross Sea. It is unlikely that prey
318 distribution was a factor limiting the occupation of the Ross Sea by elephant seals during the

319 late Holocene, as they forage in this region today but return to the sub-Antarctic to breed and
320 moult (Hall *et al.*, 2006).

321 If ice-free breeding habitat suitable for elephant seals was available during the mid to late
322 Holocene in the Ross Sea, then it may have also been suitable for king penguin occupation.
323 However, no king penguin remains have been discovered in the region. The most probable
324 explanation is that king penguins did not venture into the Ross Sea for foraging, and therefore
325 did not have the opportunity to discover emergent breeding habitat in the region. Today, king
326 penguins from Macquarie Island forage almost exclusively in the Polar Frontal Zone, well
327 north of the Ross Sea (Sokolov *et al.*, 2006). While Macquarie Island elephant seals often
328 forage in the Polar Frontal Zone, they also forage much further south over the Antarctic
329 continental shelf and in the Ross Sea (Bradshaw *et al.*, 2003, Charrassin *et al.*, 2008, Hindell
330 *et al.*, 1991). It appears that the wide-ranging foraging habits of the elephant seal may convey
331 an advantage in discovering newly available breeding habitat.

332 Given that many of the sub-Antarctic islands that are currently host to elephant seal breeding
333 colonies were probably glaciated and/or surrounded by sea ice during the LGM (Gersonde *et*
334 *al.*, 2005, Hodgson *et al.*, 2014), it is likely that elephant seal populations were either reduced
335 in size or displaced northwards, possibly to continental South America, which is currently
336 home to several Southern elephant seal breeding colonies (Lewis *et al.*, 2006, Thatje *et al.*,
337 2008) and may have been occupied by the species during the Middle Pleistocene, based on
338 limited fossil evidence (Valenzuela-Toro *et al.*, 2015). The population sizes of other elephant
339 seal colonies during the LGM could be investigated in the future using genetic coalescent
340 methods, as has been done successfully for king penguins (Trucchi *et al*., 2014).

Ice-free breeding species – the *Pygoscelis* penguins

The three *Pygoscelis* penguins are the chinstrap (*Pygoscelis antarctica*), the gentoo (*Pygoscelis papua*) and the Adélie (*Pygoscelis adeliae*). Chinstraps and gentoos currently breed in colonies on sub-Antarctic islands, the Antarctic Peninsula and maritime Antarctic islands (Figure 3c,d) (Borboroglu & Boersma, 2013), while the Adélie has a circumpolar distribution with breeding colonies located at ice-free areas of the Antarctic continent, the Antarctic Peninsula and some maritime Antarctic islands (Figure 3e) (Emslie *et al.*, 2003, Lynch & LaRue, 2014, Schwaller *et al.*, 2013). All three *Pygoscelis* species require ice-free ground for nesting (Williams, 1995). They arrive at their breeding colonies when the sea ice is most extensive (Emmerson *et al.*, 2011) and build nests out of small rocks (Williams, 1995). This reliance on ice-free ground suggests that Pygoscelids experienced a restriction of their breeding habitat during the LGM and may have retreated into glacial refugia or range-shifted to lower latitudes, at least for breeding purposes. Given that sea levels were lower during the LGM than now, it is possible that many LGM breeding sites are now submerged, making the discovery of physical evidence of these sites unlikely. The palaeoecology of the Pygoscelids has been very well studied relative to other Southern Ocean predators, with a wealth of evidence available concerning their distributions and abundances throughout the Holocene.

A common occurrence for all three Pygoscelid penguins throughout the Holocene is the regular shifting of colony sites (often local altitudinal shifts) in response to fluctuating sea levels and changing coastlines (Tatur *et al.*, 1997). A clear distinction must be made between the effects of climatic changes, such as changes in sea ice conditions, glaciation, prey availability or predation, as opposed to local geologic changes, such as fluctuating sea levels (Tatur *et al.*, 1997). In the first scenario, climate change may result in changes to the overall

numbers of penguins and their ranges, whereas in the second scenario, individual nesting sites could be locally relocated or abandoned even when the population is of constant size and the overall range is unchanged (Tatur *et al.*, 1997). There is evidence for local shifts of Pygoscelid colonies in response to sea level changes across their distributions (Baroni & Orombelli, 1994b, Emslie & McDaniel, 2002, Emslie *et al.*, 1998, Emslie & Woehler, 2005, Myrcha & Tatur, 1991, Stonehouse, 1970b, Tatur *et al.*, 1997). However, here we will focus on changes in the overall abundance and distribution of these species in response to large-scale climate changes.

Chinstrap penguins

A genetic coalescent study of chinstrap penguins from the Scotia Arc (West Antarctic Peninsula, South Shetland Islands, South Orkney Islands and South Sandwich Islands; Figure 3c), representing almost the entire global population of chinstrap penguins, detected a dramatic increase in chinstrap abundance during the Holocene (Clucas *et al.*, 2014). From an LGM female effective population size of *ca*. 2,000 birds, the population began to increase gradually around 10 kya and then rapidly around 7 kya, eventually reaching an effective female population size of almost 100,000 individuals, equating to a 50-fold increase in abundance (Clucas *et al.*, 2014). The increase occurred coeval with deglaciation of the species current range; deglaciation of the South Shetland Islands was underway by *ca*. 14 kya, with open marine conditions present in Maxwell Bay (adjacent to current colonies) by 10 kya (Ó Cofaigh *et al.*, 2014, Hodgson *et al.*, 2014), facilitating the initial range-expansion and gradual increase in abundance. Deglaciation of the South Orkney Islands and the Antarctic Peninsula occurred by *ca*. 7.5 kya and 6.8 kya, respectively (Ó Cofaigh *et al.*, 2014, Hodgson *et al.*, 2014), opening up further chinstrap habitat and facilitating the rapid increase in abundance from *ca*. 7 kya.

389 The evidence suggests that chinstrap penguins rapidly colonised new breeding habitat as it
390 became available during deglaciation. The locations of chinstrap colonies during the LGM
391 are unknown, but the species was most likely distributed further north than they are now, as
392 their current breeding locations were glaciated at that time. Future recovery of sub-fossil
393 remains dating to the early Holocene or LGM may shed light on the chinstrap penguin's past
394 distribution; currently only genetic coalescent data are available for this period (Table 1).

395 **Gentoo penguins**

396 Modern gentoo penguins are split into two sub-species, the northern (*Pygoscelis papua*
397 *papua)* and southern (*Pygoscelis papua ellsworthii*) gentoos, which are currently distributed
398 on either side of the Polar Front (Figure 3d) (Stonehouse, 1970a). Phylogenetic analyses
399 indicate that the two sub-species diverged either during the LGM or just after it, with their
400 most recent common ancestor dated at between 11 and 59 kya (Clucas *et al.*, 2014). There are
401 two possible scenarios for how the sub-species arose. Firstly, if the divergence occurred
402 during the LGM it is likely that the two sub-species represent two glacial refuge populations
403 that were geographically isolated during the LGM for long enough to diverge genetically
404 (Clucas *et al.*, 2014). In the second scenario, that of divergence following the end of the
405 LGM, penguins originating from a single LGM gentoo population in the north may have
406 colonised new areas south of the Polar Front as more breeding habitat became available
407 following deglaciation, thus forming the southern gentoo sub-species (Clucas *et al.*, 2014).
408 The second scenario is the more likely, as the current breeding habitat of the northern gentoo
409 penguins on the Falkland Islands was not glaciated during the LGM (Hodgson *et al.*, 2014)
410 and was also north of the maximum sea ice extent (Allen *et al*., 2011, Collins *et al*., 2012),
411 suggesting that it was ice-free and probably suitable for nesting. The Falkland Islands could
412 therefore have supported an LGM population of gentoos (Figure 3d), which were able to

413 expand south following the deglaciation of their current range from *ca*. 14 kya (for Maxwell
414 Bay, South Shetland Islands) (Ó Cofaigh *et al.*, 2014). This scenario is supported by genetic
415 coalescent analyses which indicate that while both sub-species increased in number during
416 the Holocene, the size of the northern gentoo population gradually increased by
417 approximately three-fold from *ca*. 9 kya (Clucas *et al.*, 2014), while the southern gentoos
418 increased far more rapidly, by about 70-fold commencing *ca*. 13 kya, consistent with
419 expansion into new habitat (Clucas *et al.*, 2014, Peña *et al.*, 2014). Gentoo penguin bones
420 dated at *ca*. 4.5 kya have been discovered on King George Island in the South Shetlands,
421 indicating that the island may have been occupied at this time, however, the remains were
422 adult skeletons only, therefore it is unclear whether breeding colonies were present (Del Valle
423 *et al.*, 2002). The slight increase in the northern gentoo population can probably be attributed
424 to increasing biological productivity in the Southern Ocean at this time (Anderson *et al.*,
425 2009, Denis *et al.*, 2009b, Kohfeld *et al.*, 2005).

426 **Adélie penguins**

427 The palaeoecology of Adélie penguins has been very well studied, more so than any other
428 Southern Ocean predator. Accumulations of the weathered remains of Adélie penguins were
429 first noted in the Ross Sea during the *Carsten Borkgrevink Southern Cross* expedition in 1899
430 (Emslie *et al*., 2014), and the first radiocarbon dating of sub-fossil remains was performed in
431 the 1950s (Harrington & McKellar, 1958). Many studies on the relationship between Adélie
432 penguins and climate changes followed and the topic has been recently reviewed by Emslie *et*
433 *al.* (2014), Millar *et al*. (2012) and Sun *et al*. (2013). In light of this, we will give only a brief
434 overview of Adélie penguin population changes in relation to historical climate change.

435 A pairwise sequentially Markovian coalescent analysis of an Adélie penguin genome from
436 the Ross Sea revealed a gradual increase in Adélie numbers from *ca*. 1 mya, followed by a

437 rapid increase commencing *ca*. 150 kya (Li *et al.*, 2014), in the heart of the penultimate
438 glacial period (Jouzel *et al.*, 2007). The onset of an Adélie penguin population expansion
439 during a glacial period is unexpected, as much of their contemporary Antarctic breeding
440 habitat would have been glaciated at that time. A possible explanation is that the Adélie
441 penguin breeding distribution was located further north in the past, for example on sub-
442 Antarctic islands, however, until sub-fossil remains dated to this period are discovered this
443 possibility remains necessarily speculative. The oldest remains so far discovered are *ca*.
444 45,000 years old and recovered in the Ross Sea (Emslie *et al*., 2007).

445 The abundance of Adélie penguins then declined *ca*. 60 kya during a cold period (Figure 1),
446 corresponding with reduced ice-free ground available for nesting (Li *et al.*, 2014).
447 Radiocarbon dating of remains has shown that Adélies were present in the Ross Sea as early
448 as *ca*. 45 kya, however, despite extensive radiocarbon dating from the Ross Sea, there are no
449 records of occupation during the LGM (Emslie *et al*., 2007), suggesting that the species was
450 displaced to the north and/or LGM colony sites are now submerged. Phylogenetic studies
451 found evidence of two genetic lineages that are suggestive of two refuge populations dating
452 to the LGM (Clucas *et al.*, 2014, Lambert *et al.*, 2002, Ritchie *et al.*, 2004). One of these
453 lineages was comprised solely of individuals from modern Ross Sea colonies suggesting that,
454 although no physical evidence has been discovered so far, an LGM refuge may have been
455 situated in the vicinity of the Ross Sea (Ritchie *et al.*, 2004).

456 The radiocarbon record so far indicates that Terra Nova Bay, which is located just north of
457 the Drygalski Ice Tongue, was the first area within the Ross Sea to be occupied by Adélie
458 penguins following the LGM, with colonies dated at *ca*. 8 kya (Emslie *et al*., 2007).
459 Colonisation followed very closely after deglaciation of the area, with the Ross Sea ice sheet
460 retreating from Terra Nova Bay shortly prior to 8 kya (Baroni & Hall, 2004). While

deglaciation provided the ice-free nesting habitat that Adélie penguins require, they would also have needed open water access amidst the sea ice, which is thought to have been provided by the Terra Nova Bay polynya (Berkman *et al.*, 1998, Emslie *et al.*, 2007). The polynya is currently an area of high productivity (Saggiomo *et al.*, 2002), and Terra Nova Bay is home to the only Adélie colony in the Ross Sea with a demonstrated record of continuous occupation over the past 7,000 years (Emslie *et al.*, 2007), suggesting that the locale is particularly favourable for Adélie penguins. Sediment core records indicate that the Terra Nova Bay polynya has been present since the mid Holocene, although dating the time of inception has proven difficult (Krissek, 1988). Sediments from outside the current polynya limits also show that the polynya was much larger during the mid Holocene (Cunningham *et al.*, 1999, Krissek, 1988). There was also a peak in productivity in Terra Nova Bay from 7.1−3.2 kya (Cunningham *et al.*, 1999) which could have further facilitated Adélie penguin occupation by increasing local prey resources. Dietary analysis showed that between 7.2 and 2 kya Adélie penguins in Terra Nova Bay consumed higher-trophic level prey, predominantly Antarctic silverfish (*Pleuragramma antarcticum*), before shifting towards more krill consumption after 2 kya (Lorenzini *et al.*, 2009, 2010).

A genetic coalescent study of Adélie penguin populations from the Antarctic Peninsula and Scotia Arc (Figure 3e) indicated an LGM effective population size roughly one tenth of the current population size (Clucas *et al.*, 2014). The increase in abundance began *ca*. 16 kya (Clucas *et al.*, 2014), following the end of the LGM and coinciding with deglaciation of the region (Ó Cofaigh *et al.*, 2014, Hodgson *et al.*, 2014). It is likely that Adélie penguins in this region were displaced north during the LGM and then underwent a latitudinal range-shift and population expansion as habitat became available to the south, similar to gentoo and chinstrap penguins in the same region (Clucas *et al.*, 2014). It is interesting to note that the expansion of Adélie penguins predates that of the other Pygoscelid penguins by a few thousand years

(Clucas *et al.*, 2014). A possible explanation for this is that the Adélie penguin's enhanced proclivity for sea ice compared to the other two Pygoscelid species allowed it to colonise southerly habitat at an earlier stage of sea ice retreat.

Adélie penguin nesting locations and local abundances have fluctuated regularly throughout the Holocene as glaciation and sea ice cover changed (Baroni & Orombelli, 1994b, Emslie *et al.*, 1998, 2003, 2007, Emslie & McDaniel, 2002, Emslie & Woehler, 2005, Huang *et al.*, 2009, Millar *et al.*, 2012). The extensive breeding distribution of Adélie penguins has resulted in regional variation in their ecological responses, with notable differences between the Antarctic Peninsula compared to continental Antarctica, owing to the different environmental conditions of these regions (i.e. the Antarctica Peninsula is relatively warm and moist compared to the cold, dry climate of continental Antarctica). A common finding of many of the Holocene studies is of an Adélie penguin "optimum" in continental Antarctica during the mid Holocene (*ca*. 2−5 kya), corresponding to a time of maximum Adélie penguin numbers in the Ross Sea (Baroni & Orombelli, 1994b, Emslie *et al.*, 2003, 2007), Windmill Islands (Emslie & Woehler, 2005) and Vestfold Hills (Huang *et al.*, 2009). The timing of the Adélie penguin optimum is coincident with a warm period indicated by the ice core record (Jouzel et al., 2007), and it is possible that reduced concentrations of sea ice were the driver for increased penguin occupation (Emslie *et al.*, 2003). The species is thought to occupy a narrow habitat optimum between too much sea ice (insufficient nesting habitat and access to foraging grounds) and too little sea ice (insufficient foraging habitat) (Ainley, 2002, Fraser *et al.*, 1992).

Studies of Adélie penguin diet through time and space show a remarkable flexibility in prey species consumed (Emslie & Patterson, 2007). On the Antarctic Peninsula, a study of diet since *ca*. 6 kya using physical prey remains recovered from ornithogenic soils showed that

Antarctic silverfish were preferentially consumed during cool periods, while squid (*Psychroteuthis glacialis*) were exploited more during warmer periods (Emslie & McDaniel, 2002). Similar patterns were observed at the Windmill Islands, East Antarctica, with recovered prey type fluctuating over the 9 kyr occupation period, and a notable abundance of squid remains during the mid-Holocene warm period (Emslie & Woehler, 2005). Stable isotopic analyses at the Vestfold Hills, East Antarctica, are consistent with these findings, with elevated consumption of higher-trophic level prey during warm periods, compared to more krill consumption in colder periods (Huang *et al.*, 2013). In the Ross Sea, stable isotopic analyses suggested a preference for higher-trophic level prey until 2 kya, after which time there was a shift towards more krill consumption (Lorenzini *et al.*, 2010). The Adélie penguin "optimum" coincided with periods of higher-trophic level prey consumption in East Antarctica (Huang *et al.*, 2013) and the Ross Sea (Lorenzini *et al.*, 2010). Whether an increased availability of higher-trophic level prey was a driver for Adélie penguin population expansion, or warmer climate and reduced sea ice cover drove increases in both Adélie penguins and Antarctic silverfish, is currently unclear. However, the ability of Adélie penguins to adapt their diet according to prey availability may have aided in the species' capacity to adapt to changing environmental conditions, as reflected by their widespread persistence around most of Antarctica throughout the Holocene.

Ice-free breeding species – flying seabirds of the Antarctic continent

Antarctica is home to breeding populations of several flying seabird species that nest at ice-free sites along the Antarctic coastline and offshore islands. However, historical population data are only available for the snow petrel; as such, the population trends of Antarctic flying seabirds in relation to past climate change is an area warranting much further study, given that seabirds are particularly vulnerable to projected climate change (Jenouvrier, 2013).

534 **Snow petrels**

535 Snow petrels require ice-free rock for their colony sites and typically establish nests in
536 cavities created by large boulders on nunataks, rocky hills or mountains, located anywhere
537 from the coast to up to several hundreds of kilometres inland (Figure 3f) (Ainley *et al.*, 2006,
538 Goldsworthy & Thomson, 2000, Verkulich & Hiller, 1994). The locations of snow petrel
539 nesting sites are governed by the availability of suitable cavities with access to productive
540 feeding locations, usually within a day's flight of the sea ice field (Ainley *et al.*, 2006, Fraser
541 & Ainley, 1986, Hiller *et al.*, 1988).

542 Snow petrel occupation histories are available for several locations based on radiocarbon
543 dating of mumiyo deposits. Snow petrels have been present in Dronning Maud Land from at
544 least *ca*. 37 kya (Figure 3f) and were widely distributed in the region throughout the LGM
545 (Hiller *et al.*, 1988, 1995, Steele & Hiller, 1997, Thor & Low, 2011). Interestingly, snow
546 petrels only colonised the ice-free Bunger Hills region *ca*. 10 kya (Figure 3f), after which
547 time they were continuously present in the area, with periods of rapid population expansion
548 between 6 and 8 kya and again from 2 kya (Verkulich & Hiller, 1994). The timing of the
549 initial colonisation of the region is noteworthy, as the inner region of the Bunger Hills was
550 partially deglaciated both prior to and during the LGM (Gore *et al.*, 2001, Mackintosh *et al.*,
551 2014), indicating that ice-free nesting sites were probably available and, therefore, that
552 alternative factors may have prevented snow petrel colonisation of this area prior to 10 kya.

553 Access to feeding grounds may have limited the locations of snow petrel colonies during the
554 glacial period and early Holocene, when a combination of the East Antarctic Ice Sheet
555 expansion (Mackintosh *et al.,* 2011) and greater sea ice extent (Gersonde *et al.*, 2005) placed
556 open water further from terrestrial nesting sites (Figure 1). At the Bunger Hills, mumiyo
557 deposits spanning the last *ca*. 10 kyr have been analysed for stable isotopes and compared

with the isotopic variation in a nearby marine sediment core within the snow petrels' foraging range (Ainley *et al*., 2006). The isotopic signatures indicated that during the early Holocene (9.5 – 8.5 kya) snow petrels were consuming pelagic (rather than neritic) prey, suggesting that they were foraging further offshore, presumably forced by the expansive sea ice field (Ainley *et al*., 2006). From 8.5 kya onward, the isotopic record is consistent with consumption of neritic prey and, therefore, a foraging range closer to the continent (Ainley *et al*., 2006).

It has been proposed that snow petrel persistence in Dronning Maud Land throughout the LGM was made possible by polynyas proximate to the coast that provided feeding grounds (Hiller *et al.*, 1988, Thatje *et al.*, 2008). There is sediment core evidence for polynyas in this region during the LGM, the nearest of which is only 300 km from the LGM nesting sites in Dronning Maud Land (Figure 3f) (Thatje *et al.*, 2008). There is no evidence of any LGM polynyas proximate to the Bunger Hills that could have supported snow petrels. Snow petrel settlement of the Bunger Hills may therefore have been limited by sea ice extent in the region, with settlement occurring in the early Holocene once sea ice had retreated, placing foraging grounds within reach of nesting sites. The Dronning Maud Land population also expanded during the Holocene; this may have been driven by sea ice retreat that provided more foraging habitat than polynyas alone, therefore supporting greater numbers of snow petrels (Hiller *et al.*, 1995). In both the Bunger Hills and Dronning Maud Land, increasing biological productivity from 10 kya (Denis *et al.*, 2009b) may have contributed to the rise in snow petrel numbers. At present, the occupation history of snow petrels has been reconstructed solely from mumiyo radiocarbon dates (Table 1); future genetic coalescent studies could shed light on the timing and magnitude of the expansions of both the Bunger Hills and Dronning Maud Land populations.

582 While the rate of snow accumulation at nesting sites is known to be a factor in the breeding
583 success of snow petrels today (Einoder *et al.*, 2014), we found no historical correlation
584 between accumulation rates and snow petrel occupation at either the Bunger Hills or
585 Dronning Maud Land, based on ice core records (Severi *et al.*, 2007, van Ommen *et al.*,
586 2004).

587 Antarctic sea ice breeders

588 Several Southern Ocean predators have life cycles that are closely tied to the seasonal
589 Antarctic sea ice field; these predators use the sea ice as a breeding platform upon which to
590 raise their offspring. These ice-dependent predators are likely to be especially vulnerable to
591 climate change (Jenouvrier *et al.*, 2014), as Antarctic sea ice is expected to undergo
592 substantial declines in the future. In the most extreme climate model scenario (RCP8.5), sea
593 ice would be completely absent from East Antarctica during February by 2081−2100 and
594 only retained in small areas of the Weddell and Ross Seas (Collins *et al.*, 2013a).

595 Emperor penguins (*Aptenodytes forsteri*) and Weddell seals (*Leptonychotes weddellii*) both
596 form breeding colonies on coastal fast ice (Figure 3g,h), whereas the leopard (*Hydrurga*
597 *leptonyx*), Ross (*Ommatophoca rossii*) and crabeater (*Lobodon carcinophagus*) seals breed
598 on icefloes within the pack ice zone (Budd, 1961, Siniff, 1991). Fast ice is the stable region
599 of sea ice that is attached to the continent, whereas pack ice drifts with the currents offshore.
600 Physical remnants of sea ice predators are scarce, as most physical remains are lost to the
601 ocean when the sea ice undergoes its annual melt. In these cases, genetic studies are
602 particularly useful.

603 **Emperor penguins**

604 Thatje *et al*. (2008) hypothesised that the emperor penguin, as the only penguin able to breed
605 on sea ice, may have flourished during the LGM when there was a lack of competition for
606 resources. However, a genetic coalescent study revealed that emperor penguins were far less
607 abundant during the LGM than they are today (Younger *et al.*, 2015). The East Antarctic
608 emperor penguin population expanded nine-fold during the Holocene from *ca*. 12 kya, while
609 the Ross Sea population expanded three-fold, commencing *ca*. 9.5 kya (Younger *et al.*,
610 2015). Given that emperor penguins breed on sea ice, it seems unlikely that breeding habitat
611 would have been a limiting factor during the LGM. However, the increased sea ice extent
612 during the LGM (Allen *et al*., 2011, Collins *et al*., 2012, Gersonde *et al.*, 2005) may have
613 restricted foraging habitat and, coupled with low biological productivity (Kohfeld *et al.*,
614 2005), could have resulted in a scarcity of prey resources.

615 Evidence for three ancestral clades originating during the LGM suggests that emperor
616 penguins were isolated within three glacial refugia at the time, one of which was most likely
617 located in or adjacent to the Ross Sea, north of the Ross Sea ice sheet (Figure 3g) (Younger *et*
618 *al.*, 2015). The other two clades had no geographic bias and have now hybridized to form a
619 single breeding population in East Antarctica (Younger *et al.*, 2015); incomplete mixing of
620 ancestral lineages in this manner is a typical indication of survival of the Pleistocene ice-ages
621 within multiple refugia (Hewitt, 1996). Interestingly, the geographic pattern of the lineages
622 mirrors that found for Adélie penguins, with one lineage restricted to the Ross Sea, while the
623 other is distributed around the continent to the Weddell Sea (Younger *et al.*, 2015).

624 It is possible that emperor penguin glacial refugia were associated with polynyas (Younger *et*
625 *al.*, 2015). Several extant colonies are located near polynyas, which are used as feeding
626 grounds during the winter months when sea ice extent is at its greatest (Croxall *et al.*, 2002).

There is evidence for several LGM polynyas in the Weddell and Ross Seas (Figure 3g) (Brambati *et al.*, 2002, Hiller *et al.*, 1988, Mackensen *et al.*, 1994, Smith *et al.*, 2010, Sprenk *et al*., 2014, Thatje *et al.*, 2008). Some of these polynyas may have sustained refugial populations of emperor penguins throughout the LGM, with populations then expanding coeval with local sea ice retreat and increasing biological productivity, which happened asynchronously between the Ross Sea and East Antarctica (Anderson *et al.*, 2009, Barbara *et al.*, 2010, Denis *et al.*, 2009a,b, Licht & Andrews, 2002, Sedwick *et al.*, 2001), accounting for the different expansion times of the two populations. Another possible limiting factor for emperor penguins was the extreme decrease in air temperatures during the LGM, which were *ca*. 13°C colder than the present day (Jouzel *et al.*, 2007). LGM air temperatures during the winter breeding months may have been near the penguins' lower limit of temperature tolerance (Le Maho *et al.*, 1978), potentially impacting breeding success and adult survival.

A pairwise sequentially Markovian coalescent analysis of an emperor penguin genome from East Antarctica indicated a gradual increase in emperor numbers from *ca*. 1 mya to 100 kya (Li *et al.*, 2014). Throughout the period of expansion the Antarctic climate went through many glacial cycles (Jouzel *et al.*, 2007, Li *et al.*, 2014), which had no noticeable effect on emperor penguin numbers. However, the effective population size during this period was less than the LGM effective population size (Li *et al.*, 2014), suggesting that emperor penguins may not have reached carrying capacity yet, possibly explaining the continued gradual growth of emperor penguin numbers even during glacial periods. Based on the pairwise sequentially Markovian coalescent method, emperor penguin effective population size was relatively stable during the LGM and Holocene (Li *et al.*, 2014); however this method is known to have low resolution over shorter timescales (i.e. tens of thousands of years), due to the infrequency of coalescent events in a single genome (Sheehan *et al.*, 2013).

651 **Weddell, crabeater and Ross seals**

652 A genetic study of ice-breeding seals from the Ross Sea determined that both Weddell and
653 crabeater seals in the region underwent historical population expansions based on a mismatch
654 distribution test using the mitochondrial control region, whereas Ross seals showed no
655 evidence of a population expansion based on the same genetic marker (Curtis *et al.*, 2009,
656 2011). Curtis *et al*. (2009) stated that population expansion occurred 731 kya for Weddell
657 seals and 1.6 mya for crabeater seals. However, these estimates are somewhat implausible,
658 being much older than expansions generally detected using the mitochondrial control region,
659 which is a rapidly evolving region of the genome typically used to detect events that occurred
660 at timescales of tens of thousands of years ago, for example, in elephant seals (de Bruyn *et*
661 *al.*, 2009). In their follow-up paper (Curtis *et al.*, 2011), the authors corrected the estimate of
662 Weddell seal expansion time to 81 kya, and stated that Curtis *et al*. (2009) had incorrectly
663 reported the expansion time in generations rather than years. However, if the expansion time
664 was 731,000 generations ago, correcting this to years would date the population expansion
665 time at 6.58 mya, based on the generation time of nine years given in Curtis *et al.* (2009),
666 which predates the speciation of Weddell seals (which split from the leopard seal between
667 1.25 and 3.63 mya (Fulton & Strobeck, 2010)), suggesting that there may also be an error in
668 the original estimate of 731,000 generations (Curtis *et al.*, 2009). Due to the uncertainty in
669 the estimates of Curtis *et al*. (2009) and (2011), the timing of the population expansions of
670 Weddell seals and crabeater seals in the Ross Sea are unclear, and it is therefore difficult to
671 postulate any underlying environmental driver.

672 A coalescent study of East Antarctic Weddell seals indicated that the effective population
673 size in this region has been stable since 80 kya (Younger, 2015). Over this period there were
674 several major changes in climatic regime, including the LGM (Figure 1) (Jouzel *et al.*, 2007).

675 The lack of response of Weddell seal abundance to these changes suggests that suitable
676 breeding and foraging habitat were available throughout this entire period. This is plausible,
677 as the Weddell seal's breeding habitat (sea ice) has been available throughout the last 80 kyr.
678 As the sea ice field expanded during glacial periods, Weddell seals may have shifted their
679 breeding distribution northwards to stay within reach of water access for foraging.

680 Key long-term drivers of Southern Ocean predator populations

681 While the timing and magnitude of population changes varied by species and location (Table
682 1), our synthesis revealed two key factors underlying long-term Southern Ocean predator
683 population changes; 1) the availability of ice-free ground for breeding, and 2) access to
684 productive foraging grounds.

685 For those species that require ice-free ground for breeding, the processes of glaciation and sea
686 ice fluctuation were key drivers of population change. The distributions and abundances of
687 elephant seals, snow petrels, gentoo, chinstrap and Adélie penguins all responded strongly to
688 the emergence of new breeding habitat as deglaciation and reductions in sea ice opened up
689 new ice-free areas. The rate and extent of range-shifts in response to new breeding habitat
690 appear to be constrained both by the relative environmental tolerance of the species as well as
691 its mobility. For example, Adélie penguins are more tolerant to sea ice than chinstrap or
692 gentoo penguins and were therefore able to expand earlier in the warming period. The wide-
693 ranging elephant seal took swift advantage of emergent habitat 2,500 km from its main
694 breeding grounds, while the less mobile king penguin did not. This finding highlights the
695 need to take a species' environmental tolerance, dispersal ability and current foraging range
696 into account when considering future range-shifts.

Access to productive foraging grounds was another limiting factor for Southern Ocean predator populations. King penguins, snow petrels and emperor penguins all had breeding habitat available to them during the LGM, yet their numbers were much smaller than today. Lower biological productivity of the Southern Ocean during the LGM is likely to have reduced overall prey abundance. Additionally, the proximity of feeding grounds to breeding sites may have been reduced. The preferred foraging grounds of the king penguins are the polar fronts, which were shifted latitudinally northwards during the LGM. Snow petrels breed on the Antarctic continent and fly to the ocean for foraging; during the LGM, the increased sea ice extent placed open water access further away. In the case of the snow petrel, it appears that colonies only persisted in regions that were proximate to polynyas, which could have facilitated foraging. These findings highlight the importance of productive foraging grounds proximate to breeding locations for Southern Ocean predators. With the physical and biological changes that are currently occurring in the Southern Ocean, management bodies need to recognise the importance of foraging grounds in reach of breeding sites and act to minimise potential impacts in these areas from human activities such as fisheries or pollution.

Our synthesis suggests that polynyas may have played an important role as seabird refugia in the past. The range of snow petrels was reduced during the LGM, with a colony persisting in Dronning Maud Land adjacent to a polynya in the region. The locations of Adélie and emperor penguin refugia were most likely in the vicinity of known LGM polynyas adjacent to the Ross Sea. The role of polynyas as past refugia could be further investigated in the future via genetic analyses of other seabird species, in combination with more complete sediment core records to indicate the locations and sizes of polynyas during the LGM. Given existing evidence of the importance of polynyas in the past, and their high biological productivity in general, it is possible that polynyas could act as future Southern Ocean predator refugia and should therefore be considered in any future management for conservation in the Antarctic.

722 Interestingly, some Southern Ocean predators showed no response to climate cycling.
723 Indications that the Weddell seal has maintained a constant population size in East Antarctica
724 over the past 80 kyr are remarkable, and suggest a robustness of the species to climate
725 changes in the past. However, it should be noted that at all times during the past 80 kyr
726 suitable breeding habitat, in the form of extensive sea ice, was available. Future projections
727 of sea ice decline may mean that the Weddell seal, which has been so robust to climate
728 cycling in the past, is now under threat.

729 Future palaeoecological studies could fill several key gaps in our understanding of the
730 climate change responses of Southern Ocean predators. Pack ice seals, including the Ross,
731 crabeater and leopard seals, breed on pack ice and are therefore vulnerable to declines in sea
732 ice extent, but their responses to past climate regime shifts are largely unknown. It is possible
733 that they may be robust to climate changes, as their fast ice breeding cousins the Weddell
734 seals were, however, their pack ice breeding habitat is different to fast ice. Genetic coalescent
735 and phylogenetic studies across these species' ranges could provide crucial information
736 regarding key environmental drivers of their abundances and distributions, their sensitivities
737 to climate change, and identify past refugia that could be used as potential refugia in the
738 future.

739 Conclusions and implications

740 Contemporary ecological studies suggest that the availability of suitable breeding habitat and
741 access to productive foraging grounds are crucial to the success of Southern Ocean predator
742 populations in the short-term (i.e. over decadal timescales). Our synthesis of the
743 palaeoecological data highlights the importance of these same variables over millennial
744 timescales, and suggests that the availability of suitable breeding habitat proximate to

productive foraging grounds was the major driver of change in Southern Ocean predator populations historically. Current climate models project substantial changes in both the breeding and foraging habitats of Southern Ocean predators (Collins *et al.*, 2013a, Constable *et al.*, 2014), and the palaeoecological data suggest that these are likely to drive long-term changes in the distributions and abundances of most Southern Ocean predators.

The effects of current and projected environmental changes on Southern Ocean predators have been thoroughly reviewed elsewhere (e.g. Ainley *et al.*, 2010, Constable *et al.*, 2014, Forcada & Trathan, 2009, Siniff *et al.*, 2008), as have the compounding effects of other anthropogenic forcings, such as competition for prey with commercial fisheries (Forcada *et al.*, 2012, Trathan *et al.*, 2015). Therefore, we will give only a brief overview of potential future long-term population trends based on the key drivers identified in our synthesis.

Many of the Southern Ocean predators reviewed here are likely to experience population declines and range contractions in the future. King penguin numbers may decrease as a result of a southerly displacement of the oceanographic fronts that they rely on as foraging grounds, for example, the travelling distance for brooding individuals from the Crozet Archipelago to frontal features will have doubled by 2100 (Péron *et al.*, 2012). Emperor penguins and Weddell seals will experience a loss of breeding habitat as sea ice declines in the future, and numbers of both species are likely to decrease in the long-term (Ainley *et al.*, 2010, Jenouvrier *et al.*, 2014, Siniff *et al.*, 2008). The Weddell seal has shown a remarkable robustness to climate cycling over the past 80,000 years, but whether this resilience will hold in the face of widespread breeding habitat loss is unclear. Emperor penguins and Weddell seals are also likely to alter their distributions as colonies relocate to stay on sea ice that is sufficiently stable for breeding (Ancel *et al.*, 2014, Barbraud *et al.*, 2011, LaRue *et al.*, 2015).

768 The emperor penguin has demonstrated the ability to contract its range into refugia to endure
769 adverse environmental periods in the past, and may do so again in the future.

770 Other Southern Ocean predators may increase in either range or abundance under future
771 climate change scenarios. Southern elephant seals may benefit from reduced sea ice
772 conditions as they did earlier in the Holocene, with indications that the species is already
773 expanding its range at the Antarctic Peninsula in response to local reductions in sea ice
774 (Siniff *et al.*, 2008). The Macquarie Island elephant seal population has demonstrated
775 population growth in years with a reduced sea ice field south of the island, thought to be a
776 result of favourable foraging conditions (van den Hoff *et al.*, 2014). Adélie penguin
777 populations in some locales will likely expand their breeding range inline with deglaciation,
778 as already observed at the Beaufort Island colony in the Ross Sea in recent decades (LaRue *et*
779 *al.*, 2013). However, Adélie populations in areas with large reductions in sea ice are expected
780 to decline (Ainley *et al.*, 2010), as has been observed at the Antarctic Peninsula and Scotia
781 Arc in recent years (Lynch & LaRue, 2014, Lynch *et al.*, 2012, Trivelpiece *et al.*, 2011).
782 Adélie penguins demonstrated the ability to adapt their diet to different prey types according
783 to availability throughout the Holocene, and this flexibility may aid in their long-term
784 prospects as the Antarctic food web changes in the future. Gentoo penguins, which do not
785 have the same tolerance for sea ice as the sympatric Adélie penguins, rapidly colonised new
786 breeding habitat during the Holocene as ice sheets and sea ice retreated, and a similar range
787 expansion and abundance increase is now underway at the Antarctic Peninsula and expected
788 to continue into the future (Casanovas *et al.*, 2015, Lynch *et al.*, 2012). Chinstrap penguins,
789 which we may have expected to respond favourably to ice sheet and sea ice retreat based on
790 the available palaeoecological data, are currently in decline across their distribution (Lynch *et*
791 *al.*, 2012, Trivelpiece *et al.*, 2011). The cause of the current decline is thought to be a
792 reduction in abundance of krill, the chinstrap's main prey source, as a result of fisheries and

793 the recovery of baleen whale populations (Trivelpiece *et al.*, 2011). Whether the chinstrap is
794 capable of dietary flexibility is currently unknown and stable isotope studies to elucidate
795 palaeoecological dietary trends could shed light on this.

796 Overall, our findings suggest that while the underlying drivers of population change are
797 similar across most Southern Ocean predators, the responses of species to environmental
798 change vary because of species specific factors such as dispersal ability, environmental
799 sensitivity and dietary flexibility. These interspecific differences should be considered in
800 future management and conservation plans for the Southern Ocean. As the Earth shifts into
801 the Anthropocene and faces unprecedented extinction rates and environmental change,
802 understanding the long-term drivers of species' abundances and distributions will be crucial
803 to developing effective management strategies. Comparative palaeoecological studies can
804 provide valuable insight into the key environmental drivers underlying changes in species'
805 abundance and distribution and, in combination with contemporary ecological studies, will be
806 invaluable to future conservation strategies.

807 ## Acknowledgements

808 We thank John van den Hoff, Gemma Clucas, Tom Hart, Barbara Wienecke and Mark
809 Hindell for helpful discussions regarding Southern Ocean predator population dynamics, and
810 three anonymous reviewers for their excellent suggestions for the improvement of our
811 manuscript. This research was funded by the Australian Antarctic Science Program (Project
812 4184: KM, LE and JY), the ANZ Trustees Holsworth Wildlife Research Endowment (JY)
813 and the Sea World Research and Rescue Foundation (KM and JY).

814 # References

815 Ainley D (2002) *The Adélie penguin: Bellwether of climate change,* New York, Columbia
816 University Press.

817 Ainley D, Hobson K, Crosta X, Rau G, Wassenaar L, Augustinus P (2006) Holocene
818 variation in the Antarctic coastal food web: linking δD and $\delta^{13}C$ in snow petrel diet and
819 marine sediments. *Marine Ecology Progress Series,* **306**, 31-40.

820 Ainley D, Russel J, Jenouvrier S, Woehler E, Lyver PB, Fraser W, Kooyman G (2010)
821 Antarctic penguin response to habitat change as Earth's troposphere reaches 2°C above
822 preindustrial levels. *Ecological Monographs,* **80**, 49-66.

823 Allen CS, Pike J, Pudsey CJ (2011) Last glacial–interglacial sea-ice cover in the SW Atlantic
824 and its potential role in global deglaciation. *Quaternary Science Reviews,* **30**, 2446-2458.

825 Ancel A, Cristofari R, Fretwell PT *et al.* (2014) Emperors in hiding: When ice-breakers and
826 satellites complement each other in Antarctic exploration. *PLoS One,* **9**, e100404.

827 Anderson JB, Conway H, Bart PJ *et al.* (2014) Ross Sea paleo-ice sheet drainage and
828 deglacial history during and since the LGM. *Quaternary Science Reviews,* **100**, 31-54.

829 Anderson JB, Shipp SS, Lowe AL, Wellner JS, Mosola AB (2002) The Antarctic Ice Sheet
830 during the last glacial maximum and its subsequent retreat history: a review. *Quaternary*
831 *Science Reviews,* **21**, 49-70.

832 Anderson R, Ali S, Bradtmiller L, Nielsen S, Fleisher M, Anderson B, Burckle L (2009)
833 Wind-driven upwelling in the Southern Ocean and the deglacial rise in atmospheric CO_2.
834 *Science,* **323**, 1443-1448.

835 Atkinson A, Siegel V, Pakhomov E, Rothery P (2005) Long-term decline in krill stock and
836 increase in salps within the Southern Ocean. *Nature,* **432**, 100-103.

837 Barbara L, Crosta X, Massé G, Ther O (2010) Deglacial environments in eastern Prydz Bay,
838 East Antarctica. *Quaternary Science Reviews,* **29**, 2731-2740.

839 Barbraud C, Gavrilo M, Mizin Y, Weimerskirch H (2011) Comparison of emperor penguin
840 declines between Pointe Géologie and Haswell Island over the past 50 years. *Antarctic*
841 *Science,* **23**, 461-468.

842 Barnosky AD, Matzke N, Tomiya S *et al.* (2011) Has the Earth's sixth mass extinction
843 already arrived? *Nature,* **471**, 51-57.

844 Baroni C, Hall BL (2004) A new Holocene relative sea level curve for Terra Nova Bay,
845 Victoria Land, Antarctica. *Journal of Quaternary Science,* **19**, 377-396.

846 Baroni C, Orombelli G (1991) Holocene raised beaches at Terra Nova Bay, Victoria Land,
847 Antarctica. *Quaternary Research,* **36**, 157-177.

848 Baroni C, Orombelli G (1994a) Holocene glacier variations in the Terra Nova Bay area
849 (Victoria Land, Antarctica). *Antarctic Science,* **6**, 497-505.

850 Baroni C, Orombelli G (1994b) Abandoned penguin rookeries as Holocene paleoclimatic
851 indicators in Antarctica. *Geology,* **22**, 23-26.

852 Baum JK, Worm B (2009) Cascading top-down effects of changing oceanic predator
853 abundances. *Journal of Animal Ecology,* **78**, 699-714.

854 Bentley MJ, Ó Cofaigh C, Anderson JB *et al.* (2014) A community-based geological
855 reconstruction of Antarctic Ice Sheet deglaciation since the last glacial maximum.
856 *Quaternary Science Reviews,* **100**, 1-9.

857 Berkman PA, Andrews JT, Björck S *et al.* (1998) Circum-Antarctic coastal environmental
858 shifts during the Late Quaternary reflected by emerged marine deposits. *Antarctic Science,*
859 **10**, 345-362.

860 Böning CW, Dispert A, Visbeck M, Rintoul S, Schwarzkopf FU (2008) The response of the
861 Antarctic Circumpolar Current to recent climate change. *Nature Geoscience,* **1**, 864-869.

862 Borboroglu PG, Boersma PD (2013) *Penguins: Natural history and conservation*, University
863 of Washington Press.

864 Bost C-A, Charrassin J-B, Clerquin Y, Ropert-Coudert Y, Le Maho Y (2004) Exploitation of
865 distant marginal ice zones by king penguins during winter. *Marine Ecology Progress Series,*
866 **283**, 293-297.

867 Bost C-A, Cotté C, Bailleul F *et al.* (2009) The importance of oceanographic fronts to marine
868 birds and mammals of the southern oceans. *Journal of Marine Systems,* **78**, 363-376.

869 Bost C, Delord K, Barbraud C, Cotté C, Péron C, Weimerskirch H (2013) King penguin. In:
870 *Penguins: Natural history and conservation.* (eds Borboroglu PG, Boersma PD). Seattle,
871 University of Washington Press.

872 Bracegirdle TJ, Connolley WM, Turner J (2008) Antarctic climate change over the twenty
873 first century. *Journal of Geophysical Research: Atmospheres (1984-2012),* **113**, D3.

874 Bradshaw CJ, Hindell MA, Best NJ, Phillips KL, Wilson G, Nichols PD (2003) You are what
875 you eat: Describing the foraging ecology of southern elephant seals (*Mirounga leonina*) using

876 blubber fatty acids. *Proceedings of the Royal Society of London B: Biological Sciences,* **270**,
877 1283-1292.

878 Brambati A, Melis R, Quaia T, Salvi G (2002) Late Quaternary climatic changes in the Ross
879 Sea area, Antarctica. *Antarctica at the Close of the Millennium. Royal Society New Zealand,*
880 *Wellington*, 359-364.

881 Budd GM (1961) The biotopes of emperor penguin rookeries. *Emu,* **61**, 171-189.

882 Casanovas P, Naveen R, Forrest S, Poncet J, Lynch HJ (2015) A comprehensive coastal
883 seabird survey maps out the front lines of ecological change on the western Antarctic
884 Peninsula. *Polar Biology*, **38**, 927-940.

885 Charrassin J-B, Hindell M, Rintoul S *et al.* (2008) Southern Ocean frontal structure and sea-
886 ice formation rates revealed by elephant seals. *Proceedings of the National Academy of*
887 *Sciences,* **105**, 11634-11639.

888 Clark PU, Dyke AS, Shakun JD *et al.* (2009) The last glacial maximum. *Science,* **325**, 710-
889 714.

890 Clucas GV, Dunn MJ, Dyke G *et al.* (2014) A reversal of fortunes: Climate change 'winners'
891 and 'losers' in Antarctic Peninsula penguins. *Scientific Reports,* **4**, 5024.

892 Cohen K, Finney S, Gibbard P, Fan J-X (2013) The ICS international chronostratigraphic
893 chart. *Episodes,* **36**, 199-204.

894 Collins LG, Allen CS, Pike J, Hodgson DA, Weckström K, Massé G (2013b) Evaluating
895 highly branched isoprenoid (HBI) biomarkers as a novel Antarctic sea-ice proxy in deep
896 ocean glacial age sediments. *Quaternary Science Reviews,* **79**, 87-98.

897 Collins M, Knutti R, Arblaster J *et al.* (2013a) Long-term climate change: Projections,
898 commitments and irreversibility. In: *Climate change 2013: The physical science basis.*
899 *Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental*
900 *Panel on Climate Change.* (eds Stocker TF, Qin D, Plattner G-K, Tignor M, Allen SK,
901 Boschung J, Nauels A, Xia Y, Bex V, Midgley PM) pp 1029–1136. Cambridge, United
902 Kingdom and New York, NY, USA, Cambridge University Press.

903 Collins LG, Pike J, Allen CS, Hodgson DA (2012) High-resolution reconstruction of
904 southwest Atlantic sea-ice and its role in the carbon cycle during marine isotope stages 3 and
905 2. *Paleoceanography,* **27**, PA3217.

906 Comiso J, Gordon A (1987) Recurring polynyas over the Cosmonaut Sea and the Maud Rise.
907 *Journal of Geophysical Research: Oceans (1978–2012),* **92**, 2819-2833.

908 Constable AJ, Melbourne-Thomas J, Corney SP *et al.* (2014) Climate change and Southern
909 Ocean ecosystems I: How changes in physical habitats directly affect marine biota. *Global*
910 *Change Biology,* **20**, 3004-3025.

911 Conway H, Hall BL, Denton GH, Gades AM, Waddington ED (1999) Past and future
912 grounding-line retreat of the West Antarctic Ice Sheet. *Science,* **286**, 280-283.

913 Crosta X, Denis D, Ther O (2008) Sea ice seasonality during the Holocene, Adélie Land, East
914 Antarctica. *Marine Micropaleontology,* **66**, 222-232.

915 Crosta X, Sturm A, Armand L, Pichon JJ (2004) Late Quaternary sea ice history in the Indian
916 sector of the Southern Ocean as record by diatom assemblages. *Marine Micropaleontology,*
917 **50**, 209-223.

Croxall JP, Trathan PN, Murphy EJ (2002) Environmental change and Antarctic seabird populations. *Science,* **297**, 1510-1514.

Cunningham WL, Leventer A, Andrews JT, Jennings AE, Licht KJ (1999) Late Pleistocene-Holocene marine conditions in the Ross Sea, Antarctica: evidence from the diatom record. *The Holocene,* **9**, 129-139.

Curtis C, Stewart BS, Karl SA (2009) Pleistocene population expansions of Antarctic seals. *Molecular Ecology,* **18**, 2112-2121.

Curtis C, Stewart BS, Karl SA (2011) Genetically effective population sizes of Antarctic seals estimated from nuclear genes. *Conservation Genetics,* **12**, 1435–1446.

de Bruyn M, Hall BL, Chauke LF, Baroni C, Koch PL, Hoelzel AR (2009) Rapid response of a marine mammal species to Holocene climate and habitat change. *PLoS Genetics,* **5**, e1000554.

de Bruyn M, Hoelzel AR, Carvalho GR, Hofreiter M (2011) Faunal histories from Holocene ancient DNA. *Trends in Ecology and Evolution,* **26**, 405-413.

de Bruyn M, Pinsky ML, Hall B, Koch P, Baroni C, Hoelzel AR (2014) Rapid increase in southern elephant seal genetic diversity after a founder event. *Proceedings of the Royal Society B: Biological Sciences,* **281**, 20133078.

de Vernal A, Gersonde R, Goosse H, Seidenkrantz M-S, Wolff EW (2013) Sea ice in the paleoclimate system: The challenge of reconstructing sea ice from proxies–an introduction. *Quaternary Science Reviews,* **79**, 1-8.

938 Del Valle R, Montalti D, Inbar M (2002) Mid-Holocene macrofossil-bearing raised marine
939 beaches at Potter Peninsula, King George Island, South Shetland Islands. *Antarctic Science,*
940 **14**, 263-269.

941 Denis D, Crosta X, Schmidt S *et al.* (2009a) Holocene glacier and deep water dynamics,
942 Adélie Land region, East Antarctica. *Quaternary Science Reviews,* **28**, 1291-1303.

943 Denis D, Crosta X, Schmidt S *et al.* (2009b) Holocene productivity changes off Adélie Land
944 (East Antarctica). *Paleoceanography,* **24**, PA3207.

945 Drummond AJ, Rambaut A, Shapiro B, Pybus OG (2005) Bayesian coalescent inference of
946 past population dynamics from molecular sequences. *Molecular Biology and Evolution,* **22**,
947 1185-1192.

948 Einoder L, Emmerson L, Southwell D, Southwell C (2014) Cavity characteristics and ice
949 accumulation affect nest selection and breeding in snow petrels (*Pagodroma nivea*). *Marine*
950 *Ornithology,* **42**, 175-182.

951 Emmerson L, Pike R, Southwell C (2011) Reproductive consequences of environment-driven
952 variation in Adélie penguin breeding phenology. *Marine Ecology Progress Series,* **440**, 203-
953 216.

954 Emslie SD, Berkman PA, Ainley DG, Coats L, Polito M (2003) Late-Holocene initiation of
955 ice-free ecosystems in the southern Ross Sea, Antarctica. *Marine Ecology Progress Series,*
956 **262**, 19-25.

957 Emslie SD, Coats L, Licht K (2007) A 45,000 yr record of Adélie penguins and climate
958 change in the Ross Sea, Antarctica. *Geology,* **35**, 61-64.

959 Emslie SD, Fraser W, Smith RC, Walker W (1998) Abandoned penguin colonies and
960 environmental change in the Palmer Station area, Anvers Island, Antarctic Peninsula.
961 *Antarctic Science,* **10**, 257-268.

962 Emslie SD, McDaniel J (2002) Adélie penguin diet and climate change during the middle to
963 late Holocene in northern Marguerite Bay, Antarctic Peninsula. *Polar Biology,* **25**, 222-229.

964 Emslie SD, Patterson WP (2007) Abrupt recent shift in $\delta^{13}C$ and $\delta^{15}N$ values in Adélie
965 penguin eggshell in Antarctica. *Proceedings of the National Academy of Sciences,* **104**,
966 11666-11669.

967 Emslie S, Polito M, Brasso R, Patterson W, Sun L (2014) Ornithogenic soils and the
968 paleoecology of pygoscelid penguins in Antarctica. *Quaternary International,* **352**, 4-15.

969 Emslie SD, Polito MJ, Patterson WP (2013) Stable isotope analysis of ancient and modern
970 gentoo penguin egg membrane and the krill surplus hypothesis in Antarctica. *Antarctic*
971 *Science,* **25**, 213-218.

972 Emslie SD, Woehler EJ (2005) A 9,000-year record of Adélie penguin occupation and diet in
973 the Windmill Islands, East Antarctica. *Antarctic Science,* **17**, 57-66.

974 Forcada J, Trathan PN (2009) Penguin responses to climate change in the Southern Ocean.
975 *Global Change Biology,* **15**, 1618-1630.

976 Forcada J, Trathan PN, Boveng PL *et al.* (2012) Responses of Antarctic pack-ice seals to
977 environmental change and increasing krill fishing. *Biological Conservation,* **149**, 40-50.

978 Fulton TL, Strobeck C (2010) Multiple fossil calibrations, nuclear loci and mitochondrial
979 genomes provide new insight into biogeography and divergence timing for true seals
980 (*Phocidae, Pinnipedia*). *Journal of Biogeography,* **37**, 814-829.

981 Fraser WR, Ainley DG (1986) Ice edges and seabird occurrence in Antarctica. *BioScience*,
982 258-263.

983 Fraser WR, Trivelpiece WZ, Ainley DG, Trivelpiece SG (1992) Increases in Antarctic
984 penguin populations: reduced competition with whales or a loss of sea ice due to
985 environmental warming? *Polar Biology,* **11**, 525-531.

986 Gersonde R, Crosta X, Abelmann A, Armand L (2005) Sea-surface temperature and sea ice
987 distribution of the Southern Ocean at the EPILOG last glacial maximum—a circum-Antarctic
988 view based on siliceous microfossil records. *Quaternary Science Reviews,* **24**, 869-896.

989 Gersonde R, Zielinski U (2000) The reconstruction of late Quaternary Antarctic sea-ice
990 distribution−the use of diatoms as a proxy for sea-ice. *Palaeogeography, Palaeoclimatology,*
991 *Palaeoecology,* **162**, 263-286.

992 Goldsworthy P, Thomson P (2000) An extreme inland breeding locality of snow petrels
993 (*Pagodroma nivea*) in the southern Prince Charles Mountains, Antarctica. *Polar Biology,* **23**,
994 717-720.

995 Gore D, Rhodes E, Augustinus P, Leishman M, Colhoun E, Rees-Jones J (2001) Bunger
996 Hills, East Antarctica: ice free at the last glacial maximum. *Geology,* **29**, 1103-1106.

997 Hall B, Hoelzel A, Baroni C, Denton G, Le Boeuf B, Overturf B, Töpf A (2006) Holocene
998 elephant seal distribution implies warmer-than-present climate in the Ross Sea. *Proceedings*
999 *of the National Academy of Sciences,* **103**, 10213-10217.

1000 Hall BL (2009) Holocene glacial history of Antarctica and the sub-Antarctic islands.
1001 *Quaternary Science Reviews,* **28**, 2213-2230.

1002 Harrington H, Mckellar I (1958) A radiocarbon date for penguin colonization of Cape Hallett,
1003 Antarctica. *New Zealand Journal of Geology and Geophysics,* **1**, 571-576.

1004 Heimark RJ, Heimark GM (1986) Southern elephant seal pupping at Palmer Station,
1005 Antarctica. *Journal of Mammalogy,* **67**, 189-190.

1006 Heithaus MR, Frid A, Wirsing AJ, Worm B (2008) Predicting ecological consequences of
1007 marine top predator declines. *Trends in Ecology and Evolution,* **23**, 202-210.

1008 Hewitt G (1996) Some genetic consequences of ice ages, and their role in divergence and
1009 speciation. *Biological Journal of the Linnean Society,* **58**, 247-276.

1010 Hewitt G (2000) The genetic legacy of the Quaternary ice ages. *Nature,* **405**, 907-913.

1011 Hillenbrand C-D, Bentley MJ, Stolldorf TD *et al.* (2014) Reconstruction of changes in the
1012 Weddell Sea sector of the Antarctic Ice Sheet since the Last Glacial Maximum. *Quaternary*
1013 *Science Reviews,* **100**, 111-136.

1014 Hillenbrand C-D, Cortese G (2006) Polar stratification: a critical view from the Southern
1015 Ocean. *Palaeogeography, Palaeoclimatology, Palaeoecology,* **242**, 240-252.

1016 Hiller A, Hermichen WD, Wand U (1995) Radiocarbon-dated subfossil stomach oil deposits
1017 from petrel nesting sites; novel paleoenvironmental records from continental Antarctica.
1018 *Radiocarbon,* **37**, 171-180.

1019 Hiller A, Wand U, Kämpf H, Stackebrandt W (1988) Occupation of the Antarctic continent
1020 by petrels during the past 35,000 years: inferences from a ^{14}C study of stomach oil deposits.
1021 *Polar Biology,* **9**, 69-77.

1022 Hindell M, Burton H, Slip D (1991) Foraging areas of southern elephant seals, (*Mirounga*
1023 *leonina*), as inferred from water temperature data. *Marine and Freshwater Research,* **42**, 115-
1024 128.

1025 Hodgson DA, Graham AG, Roberts SJ *et al.* (2014) Terrestrial and submarine evidence for
1026 the extent and timing of the last glacial maximum and the onset of deglaciation on the
1027 maritime-Antarctic and sub-Antarctic islands. *Quaternary Science Reviews,* **100**, 137-158.

1028 Hoelzel AR (2010) Looking backwards to look forwards: Conservation genetics in a
1029 changing world. *Conservation Genetics,* **11**, 655-660.

1030 Holland D (2001) Explaining the Weddell Polynya - a large ocean eddy shed at Maud Rise.
1031 *Science,* **292**, 1697-1700.

1032 Huang T, Sun L, Long N, Wang Y, Huang W (2013) Penguin tissue as a proxy for relative
1033 krill abundance in East Antarctica during the Holocene. *Scientific Reports,* **3**, 2807.

1034 Huang T, Sun L, Wang Y, Liu X, Zhu R (2009) Penguin population dynamics for the past
1035 8,500 years at Gardner Island, Vestfold Hills. *Antarctic Science,* **21**, 571-578.

1036 Hunt GL (1991) Occurrence of polar seabirds at sea in relation to prey concentrations and
1037 oceanographic factors. *Polar Research,* **10**, 553-560.

1038 Jenouvrier S (2013) Impacts of climate change on avian populations. *Global Change Biology,*
1039 **19**, 2036-2057.

1040 Jenouvrier S, Holland M, Stroeve J, Serreze M, Barbraud C, Weimerskirch H, Caswell H
1041 (2014) Projected continent-wide declines of the emperor penguin under climate change.
1042 *Nature Climate Change*, **4**, 715-718.

1043 Jouzel J, Masson-Delmotte V, Cattani O *et al.* (2007) Orbital and millennial Antarctic climate
1044 variability over the past 800,000 years. *Science,* **317**, 793-796.

1045 Kohfeld KE, Le Quéré C, Harrison SP, Anderson RF (2005) Role of marine biology in
1046 glacial-interglacial CO_2 cycles. *Science,* **308**, 74-78.

1047 Krissek L (1988) Sedimentation history of the Terra Nova Bay region, Ross Sea, Antarctica.
1048 *Antarctic Journal of the United States,* **23**, 104-105.

1049 Lambert DM, Ritchie PA, Millar CD, Holland B, Drummond AJ, Baroni C (2002) Rates of
1050 evolution in ancient DNA from Adelie penguins. *Science,* **295**, 2270-2273.

1051 LaRue M, Ainley DG, Swanson M, Dugger KM, Lyver PB, Barton K, Ballard G (2013)
1052 Climate change winners: Receding ice fields facilitate colony expansion and altered
1053 dynamics in an Adélie penguin metapopulation. *PLoS One,* **8**, e60568.

1054 LaRue M, Kooyman G, Lynch H, Fretwell P (2015) Emigration in emperor penguins:
1055 Implications for interpretation of long-term studies. *Ecography,* **38**, 114-120.

1056 Le Maho Y, Delclitte P, Chatonnet J (1978) Thermoregulation in fasting emperor penguins
1057 under natural conditions. *American Journal of Physiology*, 913-922.

1058 Lewis M, Campagna C, Marin M, Fernandez T (2006) Southern elephant seals north of the
1059 Antarctic Polar Front. *Antarctic Science,* **18**, 213-221.

1060 Lewis SL, Maslin MA (2015) Defining the Anthropocene. *Nature,* **519**, 171-180.

1061 Li C, Zhang Y, Li J *et al.* (2014) Two Antarctic penguin genomes reveal insights into their
1062 evolutionary history and molecular changes related to the Antarctic environment.
1063 *GigaScience,* **3**, 1-15.

1064 Li H, Durbin R (2011) Inference of human population history from individual whole-genome
1065 sequences. *Nature,* **475**, 493-496.

1066 Licht KJ, Andrews JT (2002) The ^{14}C record of Late Pleistocene ice advance and retreat in
1067 the central Ross Sea, Antarctica. *Arctic, Antarctic, and Alpine research,* **34**, 324-333.

1068 Lorenzini S, Baroni C, Fallick AE, Baneschi I, Salvatore MC, Zanchetta G, Dallai L (2010)
1069 Stable isotopes reveal Holocene changes in the diet of Adélie penguins in Northern Victoria
1070 Land (Ross Sea, Antarctica). *Oecologia,* **164**, 911-919.

1071 Lorenzini S, Olmastroni S, Pezzo F, Salvatore MC, Baroni C (2009) Holocene Adélie
1072 penguin diet in Victoria Land, Antarctica. *Polar Biology,* **32**, 1077-1086.

1073 Lynch H, LaRue M (2014) First global census of the Adélie penguin. *The Auk,* **131**, 457-466.

1074 Lynch HJ, Naveen R, Trathan PN, Fagan WF (2012) Spatially integrated assessment reveals
1075 widespread changes in penguin populations on the Antarctic Peninsula. *Ecology,* **93**, 1367-
1076 1377.

1077 Mackensen A, Grobe H, Hubberten H-W, Kuhn G (1994) Benthic foraminiferal assemblages
1078 and the δ13C-signal in the Atlantic sector of the Southern Ocean: Glacial-to-interglacial
1079 contrasts. In: *Carbon cycling in the glacial ocean: constraints on the ocean's role in global*
1080 *change.* pp 105-144. Springer.

1081 Mackintosh A, Golledge N, Domack E *et al.* (2011) Retreat of the East Antarctic ice sheet
1082 during the last glacial termination. *Nature Geoscience,* **4**, 195-202.

1083 Mackintosh AN, Verleyen E, O'Brien PE *et al.* (2014) Retreat history of the East Antarctic
1084 Ice Sheet since the last glacial maximum. *Quaternary Science Reviews,* **100**, 10-30.

1085 Martin S (2001) Polynyas. *Encyclopedia of Ocean Sciences,* **3**, 2241-2247.

1086 Mayewski P, Lyons W, Zielinski G *et al.* (1995) An ice-core-based, Late Holocene history
1087 for the Transantarctic Mountains, Antarctica. *Antarctic Research Series,* **67**, 33-45.

1088 Millar CD, Subramanian S, Heupink TH, Swaminathan S, Baroni C, Lambert DM (2012)
1089 Adélie penguins and temperature changes in Antarctica: a long-term view. *Integrative*
1090 *Zoology,* **7**, 113-120.

1091 Monnin E, Steig EJ, Siegenthaler U *et al.* (2004) Evidence for substantial accumulation rate
1092 variability in Antarctica during the Holocene, through synchronization of CO_2 in the Taylor
1093 Dome, Dome C and DML ice cores. *Earth and Planetary Science Letters,* **224**, 45-54.

1094 Moore GJ, Wienecke B, Robertson G (1999) Seasonal change in foraging areas and dive
1095 depths of breeding king penguins at Heard Island. *Polar Biology,* **21**, 376-384.

1096 Murray D (1981) The breeding of the southern elephant seal, *Mirounga leonina*, on the
1097 Antartic continent. *Polar Record,* **20**, 370-371.

1098 Myrcha A, Tatur A (1991) Ecological role of the current and abandoned penguin rookeries in
1099 the land environment of the maritime Antarctic. *Polish Polar Research,* **12**, 3-24.

1100 Ó Cofaigh C, Davies BJ, Livingstone SJ *et al.* (2014) Reconstruction of ice-sheet changes in
1101 the Antarctic Peninsula since the last glacial maximum. *Quaternary Science Reviews,* **100**,
1102 87-110.

1103 Peña F, Poulin E, Dantas GP, González-Acuña D, Petry MV, Vianna JA (2014) Have
1104 historical climate changes affected gentoo penguin (*Pygoscelis papua*) populations in
1105 Antarctica? *PLoS One,* **9**, e95375.

1106 Péron C, Weimerskirch H, Bost C-A (2012) Projected poleward shift of king penguins'
1107 (*Aptenodytes patagonicus*) foraging range at the Crozet Islands, southern Indian Ocean.
1108 *Proceedings of the Royal Society B: Biological Sciences,* **279**, 2515-2523.

1109 Pybus OG, Rambaut A, Harvey PH (2000) An integrated framework for the inference of viral
1110 population history from reconstructed genealogies. *Genetics,* **155**, 1429-1437.

1111 Ritchie PA, Millar CD, Gibb GC, Baroni C, Lambert DM (2004) Ancient DNA enables
1112 timing of the Pleistocene origin and Holocene expansion of two Adélie penguin lineages in
1113 Antarctica. *Molecular Biology and Evolution,* **21**, 240-248.

1114 Saggiomo V, Catalano G, Mangoni O, Budillon G, Carrada GC (2002) Primary production
1115 processes in ice-free waters of the Ross Sea (Antarctica) during the Austral summer 1996.
1116 *Deep Sea Research Part II: Topical Studies in Oceanography,* **49**, 1787-1801.

1117 Schwaller MR, Southwell CJ, Emmerson LM (2013) Continental-scale mapping of Adélie
1118 penguin colonies from Landsat imagery. *Remote Sensing of Environment,* **139**, 353-364.

1119 Seddon AWR, Mackay AW, Baker AG *et al.* (2014) Looking forward through the past:
1120 identification of 50 priority research questions in palaeoecology. *Journal of Ecology,* **102**,
1121 256-267.

1122 Sedwick PN, Harris PT, Robertson LG, Mcmurtry GM, Cremer MD, Robinson P (2001)
1123 Holocene sediment records from the continental shelf of MacRobertson Land, East
1124 Antarctica. *Paleoceanography,* **16**, 212-225.

1125 Severi M, Becagli S, Castellano E *et al.* (2007) Synchronisation of the EDML and EDC ice
1126 cores for the last 52 kyr by volcanic signature matching. *Climate of the Past Discussions,* **3**,
1127 409-433.

1128 Sheehan S, Harris K, Song YS (2013) Estimating variable effective population sizes from
1129 multiple genomes: a sequentially Markov conditional sampling distribution approach.
1130 *Genetics,* **194**, 647-662.

1131 Siniff DB (1991) An overview of the ecology of Antarctic seals. *American Zoologist,* **31**,
1132 143-149.

1133 Siniff DB, Garrott RA, Rotella JJ, Fraser WR, Ainley DG (2008) Projecting the effects of
1134 environmental change on Antarctic seals. *Antarctic Science,* **20**, 425-435.

1135 Smetacek V, Nicol S (2005) Polar ocean ecosystems in a changing world. *Nature,* **437**, 362-
1136 368.

1137 Smith JA, Hillenbrand C-D, Pudsey CJ, Allen CS, Graham AG (2010) The presence of
1138 polynyas in the Weddell Sea during the Last Glacial Period with implications for the
1139 reconstruction of sea-ice limits and ice sheet history. *Earth and Planetary Science Letters,*
1140 **296**, 287-298.

1141 Sokolov S, Rintoul SR (2009) Circumpolar structure and distribution of the Antarctic
1142 Circumpolar Current fronts: 2. Variability and relationship to sea surface height. *Journal of*
1143 *Geophysical Research: Oceans (1978–2012),* **114**.

1144 Sokolov S, Rintoul SR, Wienecke B (2006) Tracking the Polar Front south of New Zealand
1145 using penguin dive data. *Deep Sea Research Part I: Oceanographic Research Papers,* **53**,
1146 591-607.

1147 Sprenk D, Weber M, Kuhn G, Wennrich V, Hartmann T, Seelos K (2014) Seasonal changes
1148 in glacial polynya activity inferred from Weddell Sea varves. *Climate of the Past,* **10**, 1239-
1149 1251.

1150 Stammerjohn S, Massom R, Rind D, Martinson D (2012) Regions of rapid sea ice change: An
1151 inter-hemispheric seasonal comparison. *Geophysical Research Letters,* **39**, L06501.

1152 Steele W, Hiller A (1997) Radiocarbon dates of snow petrel (*Pagodroma nivea*) nest sites in
1153 central Dronning Maud Land, Antarctica. *Polar Record,* **33**, 29-38.

1154 Stonehouse B (1970a) Geographic variation in gentoo penguins (*Pygoscelis papua*). *Ibis,*
1155 **112**, 52-57.

1156 Stonehouse B (1970b) Recent climatic change in Antarctica suggested from ^{14}C dating of
1157 penguin remains. *Palaeogeography, Palaeoclimatology, Palaeoecology,* **7**, 341-343.

1158 Sun L, Xie Z, Zhao J (2000) Palaeoecology: A 3,000-year record of penguin populations.
1159 *Nature,* **407**, 858-858.

1160 Sun L, Emslie S, Huang T *et al.* (2013) Vertebrate records in polar sediments: Biological
1161 responses to past climate change and human activities. *Earth-Science Reviews,* **126**, 147-155.

1162 Tatur A, Myrcha A, Niegodzisz J (1997) Formation of abandoned penguin rookery
1163 ecosystems in the maritime Antarctic. *Polar Biology,* **17**, 405-417.

1164 Thatje S, Hillenbrand C-D, Mackensen A, Larter R (2008) Life hung by a thread: endurance
1165 of Antarctic fauna in glacial periods. *Ecology,* **89**, 682-692.

1166 Thor G, Low M (2011) The persistence of the snow petrel (*Pagodroma nivea*) in Dronning
1167 Maud Land (Antarctica) for over 37,000 years. *Polar Biology,* **34**, 609-613.

1168 Trathan PN, García-Borboroglu P, Boersma D *et al.* (2015) Pollution, habitat loss, fishing,
1169 and climate change as critical threats to penguins. *Conservation Biology,* **29**, 31-41.

1170 Trivelpiece WZ, Hinke JT, Miller AK, Reiss CS, Trivelpiece SG, Watters GM (2011)
1171 Variability in krill biomass links harvesting and climate warming to penguin population
1172 changes in Antarctica. *Proceedings of the National Academy of Sciences,* **108**, 7625-7628.

1173 Trucchi E, Gratton P, Whittington JD, Cristofari R, Le Maho Y, Stenseth NC, Le Bohec C
1174 (2014) King penguin demography since the last glaciation inferred from genome-wide data.
1175 *Proceedings of the Royal Society B: Biological Sciences,* **281**, 20140528.

1176 Turner J, Barrand NE, Bracegirdle TJ *et al.* (2014) Antarctic climate change and the
1177 environment: an update. *Polar Record,* **50**, 237-259.

1178 Turner J, Bindschadler RA, Convey P *et al.* (2009) Antarctic climate change and the
1179 environment. pp 526, Cambridge, Scientific Committee on Antarctic Research.

1180 Valenzuela-Toro AM, Gutstein CS, Suárez ME, Otero R, Pyenson ND (2015) Elephant seal
1181 (*Mirounga sp*.) from the Pleistocene of the Antofagasta Region, northern Chile. *Journal of*
1182 *Vertebrate Paleontology*, **35**, 918883.

1183 van Ommen TD, Morgan V, Curran MA (2004) Deglacial and Holocene changes in
1184 accumulation at Law Dome, East Antarctica. *Annals of Glaciology,* **39**, 359-365.

1185 van den Hoff J, McMahon CR, Simpkins GR, Hindell MA, Alderman R, Burton HR (2014)
1186 Bottom-up regulation of a pole-ward migratory predator population. *Proceedings of the Royal*
1187 *Society of London B: Biological Sciences*, **281**, 20132842.

1188 Verkulich SR, Hiller A (1994) Holocene deglaciation of the Bunger Hills revealed by ^{14}C
1189 measurements on stomach oil deposits in snow petrel colonies. *Antarctic Science,* **6**, 395-399.

1190 Williams TD (1995) *The penguins; Spheniscidae*, Oxford, Oxford University Press.

1191 Younger J (2015) Contrasting responses to a climate regime change by sympatric meso-
1192 predators. In: *Palaeoecological changes in populations of Antarctic ice-dependent predators*
1193 *and their environmental drivers*. pp59-85. University of Tasmania PhD, Hobart.

1194 Younger JL, Clucas GV, Kooyman G *et al.* (2015) Too much of a good thing: Sea ice extent
1195 may have forced emperor penguins into refugia during the last glacial maximum. *Global*
1196 *Change Biology,* **21**, 2215-2226.

Table 1. Summary of Southern Ocean predator population changes reviewed, including species, study location, palaeoecological data used with citations, key population trend, the proposed underlying environmental driver for population trend, and the corresponding ecological limitation.

Species	Location	Coalescent	Phylogeny	Ancient DNA	Sub-fossils	Diet	Mumiyo	Other	Population trend	Environmental driver	Ecological limitation
King penguin	Crozet Archipelago	1							Population expansion (~85x) following end of LGM	Increase in biological productivity, shift of oceanographic fronts	Prey availability
Southern elephant seal	Macquarie Island, Ross Sea	2		2,3,4	3				Range expansion to the Ross Sea 7 kya; retreat to Macquarie Island 1 kya	Retreat and advance of glacial and sea ice in the Ross Sea	Ice-free breeding habitat
Chinstrap penguin	Scotia Arc	5							Population expansion (~50x) commencing 10 kya	Deglaciation of the Scotia Arc and Antarctic Peninsula	Ice-free breeding habitat
Gentoo penguin	Scotia Arc	5,6	5		7				LGM refuge at Falkland Is, southerly range expansion and abundance increase (~70x) commencing 9 kya	Deglaciation of the Scotia Arc and Antarctic Peninsula	Ice-free breeding habitat
Adélie penguin	Scotia Arc, Ross Sea, East Antarctica, Antarctic Peninsula	5,8	9	9,10	11-16	15,17-21		22	Two glacial refugia, one in the Ross Sea; population expansion (~10x) in the Scotia Arc from 16 kya; optimum 3-5 kya	Glaciation, sea ice and sea level changes	Ice-free breeding habitat, sea ice foraging habitat
Snow petrel	Dronning Maud Land, Bunger Hills					23	23-29		Dronning Maud Land refuge during LGM, colonised Bunger Hills 10 kya	Polynyas, sea ice retreat, increasing biological productivity	Productive foraging habitat proximate to breeding locations
Emperor penguin	Ross Sea, Weddell Sea, East Antarctica	8,30	30						Three refugia during the LGM, one in the Ross Sea; population expansion (~7x) from 12 kya	Polynyas, sea ice retreat, increasing biological productivity	Productive foraging habitat proximate to breeding locations
Weddell seal	East Antarctica	31							Stable population size over the past 80 kyr	N/A	N/A

Citations referred to in Table 1: [1]Trucchi *et al.*, 2014, [2]de Bruyn *et al.*, 2009, [3]Hall *et al.*, 2006, [4]de Bruyn *et al.*, 2014, [5]Clucas *et al.*, 2014, [6]Peña *et al.*, 2014, [7]Del Valle *et al.*, 2002, [8]Li *et al.*, 2014, [9]Ritchie *et al.*, 2004, [10]Lambert *et al.*, 2002, [11]Baroni & Orombelli, 1994b, [12]Emslie *et al.*, 1998, [13]Emslie *et al.*, 2003, [14]Emslie *et al.*, 2007, [15]Emslie & Woehler, 2005, [16]Huang *et al.*, 2009, [17]Emslie & McDaniel, 2002, [18]Emslie & Patterson, 2007, [19]Huang *et al.*, 2013, [20]Lorenzini *et al.*, 2009, [21]Lorenzini *et al.*, 2010, [22]Sun *et al.*, 2013, [23]Ainley *et al.*, 2006, [24]Hiller *et al.*, 1988, [25]Hiller *et al.*, 1995, [26]Steele & Hiller, 1997, [27]Thatje *et al.*, 2008, [28]Thor & Low, 2011, [29]Verkulich & Hiller, 1994, [30]Younger *et al.*, 2015, [31]Younger, 2015

Figure Captions

Figure 1. The Antarctic temperature anomaly (the difference from the average of the last 1000 years) over the past 80,000 years. Temperatures are as estimated from the EPICA Dome C ice core (Jouzel *et al*., 2007), with the last glacial maximum (LGM) indicated by blue shading and the Holocene by green shading.

Figure 2. Map of the Antarctic and sub-Antarctic with key physical features. The approximate positions of both modern and last glacial period sea ice extents and oceanographic fronts are indicated, after (Collins *et al*., 2012, Gersonde *et al*., 2005). The summer sea ice extents (SSI) are indicated by red lines, the winter sea ice extents (WSI) by blue lines, the polar front (PF) by green lines, and the sub-Antarctic front (SAF) by yellow lines. Solid lines indicate modern features, dashed lines are the inferred locations of last glacial period features. The approximate position of the LGM ice sheet extent (LGM-IS) is indicated by a dashed orange line (Bentley *et al*., 2014). The locations of LGM polynyas are indicated by orange stars (Smith *et al*., 2010, Sprenk *et al.*, 2014).

Figure 3. Contemporary breeding distributions of Southern Ocean predators showing relevant environmental features.